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SPERMATOGENESIS IN PARATETTIX.¹

MARY T. HARMAN.

Wilson has said that "heredity is a consequence of the genetic continuity of cells by division, and the germ cells form the vehicle of transmission from one generation to another."

If this be true we should look to the structure of the germ-cells for an explanation of the phenomena that have been and are being found out in heredity. Cytologists have discovered much concerning the structure of the germ-cells and the behavior of the chromosomes during the processes of maturation and division. The combined knowledge of sex and sex ratio, and the cytological constitution of germ-cells has shown in many forms, at least, a correlation between the inheritance of sex and the dimorphism of spermatozoa or eggs, or both. However, the vast amount of cytological work has been done with forms the behavior of whose characteristics in heredity is unknown. On the other hand, much of the work in heredity has been done with forms of which little or nothing is known of the structure of the germ-cells. It is the writer's good fortune to have access to material of which some of the ancestry is known for eighteen generations, covering a period of five years.

For a number of years Dr. R. K. Nabours² has been conducting experiments with regard to inheritance in *Paratettix*, a genus of the short-horned grasshoppers. The characteristics used in his investigations are the color patterns of the pronotum and femora of the jumping legs, and the lengths of the pronotum and wings. The data show that the inheritance of the color patterns is Mendelian in its behavior. In the F₁ hybrid no part of the color pattern of one parent species is ever replaced by the color pattern of the other parent, but the color patterns of both parents are present. Reciprocal crosses give identical results. The

¹ Contribution from the Zoölogical Laboratory, Kansas State Agricultural College, No. 7.

² The writer wishes to thank Dr. R. K. Nabours for the grasshoppers which have furnished the material for this paper.

lengths of the wings and pronotum are not inherited but are closely correlated with the length of time required for the animal to reach maturity. These grasshoppers have furnished the material for the present paper.

The work on the cytological constitution of the germ-cells of *Paratettix* has been undertaken for the purpose of discovering whether or not the microscope will reveal any differences in the germ-cells of very closely related forms which may be correlated with the differences in the color pattern. The spermatogenesis of only one form (*Paratettix leuconotus-leucothorax*) is given here. *Paratettix leuconotus-leucothorax* is a hybrid, obtained by crossing *P. leuconotus* with *P. leucothorax* (or by the interbreeding of two hybrids, one being a hybrid of *leuconotus* with some other form and the other a hybrid of *leucothorax* with some other form). No attempt has been made to show any relation between the structure of the germ-cells and the somatic structures. This will be discussed in a later paper.

The chromosomal complex of the spermatogonia of *Paratettix leuconotus-leucothorax* consists of thirteen rod-shaped bodies which may be divided into two groups—one group consisting of four larger chromosomes and the other of nine smaller ones. Neither the larger nor the smaller chromosomes form equal sized pairs as Sutton has found in *Brachystola magna* and which is so frequently described for the Hemiptera and is apparently characteristic of all Diptera. All of the large chromosomes and one of the small ones are bent rods or slightly U-shaped, but the other eight are almost straight. No one of these chromosomes has been surely identified as the accessory. However, in the early prophases there is always present a mass of chromatin which has a more compact consistency and stains more intensely than the remainder of the chromatin (A, Fig. 1). This mass has not been identified with any chromosome nor is it associated with a vesicle as described by Carothers for *Arphia simplex*. There appears to be no difference in the staining capacity nor in the compactness of the chromosomes in the late prophases (Fig. 2).

The spermatogonial spindle is long and slender, and has fine but distinct fibers which converge at the poles. The centrosome

which is very distinctly visible in the metaphase stage is small and spherical. It stains almost as intensely as the chromosomes. The astral rays are short and indistinct. The chromosomes are at right angles to the spindle fibers in the metaphase stage (Fig. 7). A metaphase plate always shows one chromosome nearer the center of the spindle than any other chromosome. Sometimes it is completely surrounded by the others (Figs. 4 and 6) and sometimes merely one end is at the center of the spindle (Figs. 3 and 5). This chromosome is always one of the larger of the group of smaller ones but it is never the bent one. Few anaphase and no telophase stages have been observed. Fig. 8 shows an anaphase with rather indistinct spindle fibers, which is characteristic of all the anaphase stages observed. The centrosome, which shows distinctly in the metaphase stage (Fig. 7), is now invisible. The chromosomes are no longer at right angles to the spindle fibers but are nearly parallel with them.

Fig. 9 illustrates the condition of the cell at the beginning of the growth period. The nucleus is large and comparatively clear. Some of the chromatin is in a finely reticular condition and stains faintly with iron-haematoxylin. However, a mass of the chromatin retains the compact consistency and the density of stain of the chromosomes (*A*, Fig. 9). It has a rounded form like a nucleolus. The boundary between the nucleus and the cytoplasm is quite evident. The nucleus continues to increase in size and the reticular chromatin, which now has a greater staining capacity, forms a thread or threads having a woolly appearance. There is no polarization of the loops of the spireme but they occupy almost all of the space of the nucleus and form an irregular tangled mass. The nucleolus remains at one side of the nucleus and does not have the woolly appearance that the spireme has (Fig. 10).

In the synezeis or contraction stage, the spireme seems to shrink away from the nuclear wall, leaving a clear space between the cytoplasm and the chromatin material. There is little difference between the character of the chromatin and its staining capacity in this stage and the preceding one. The compact mass of chromatin never loses its identity and always remains at one side of the nucleus (Fig. 11). The boundary of

the nucleus soon becomes irregular, and the chromosomes of the primary spermatocyte is formed by a breaking up of the spireme thread into segments. The compact intensely staining mass which has been traced through the growth period is shown in Fig. 12 as a chromosome which differs in shape from the other chromosomes. It is ovoid and without a constriction in the middle, while all the other chromosomes are dumb-bell shaped. Not all of the chromosomes are formed at the same time. The chromatin retains its loose woolly appearance until after it has broken up into parts, then it gradually becomes more compact, takes the stain more readily and each part assumes the characteristic dumb-bell shape. While this is taking place the boundary between the nucleus and the cytoplasm becomes more irregular and by the time the chromosomes are completely formed the cytoplasm has formed a vesicle around each of them (Figs. 13 and 14).

The chromosomal complex of the primary spermatocyte consists of six dumb-bell shaped chromosomes and one ovoid chromosome. Of the six dumb-bell chromosomes two are decidedly larger than the others and one of these is much larger than the other one, as is shown in Figs. 13 to 16 inclusive. The ovoid or accessory chromosome is never among the other chromosomes but always lies near the periphery of the nucleus as it did in the growth period. When the chromosomes have become arranged on the spindle the dumb-bell chromosomes are well toward the center of the spindle, while the accessory is always near the periphery. It does not remain long in the metaphase plate but soon passes toward one pole undivided much in advance of the other chromosomes. For this reason many sections of metaphase plates show only six chromosomes and those which show seven are often cut obliquely. Not all of the chromosomes in the primary spermatocyte divide synchronously. Fig. 20 shows five of the dumb-bell chromosomes divided while the largest one shows little constriction. This division is transverse as is shown in Figs. 16 and 20. There are no loops, rings, or U's which would give the least indication of a longitudinal division. In the metaphase or early anaphases the centrosome is a small spherical body and takes the stain readily. The

spindle fibers are fine but distinct. The astral rays are similar to those of the spermatogonial divisions. In the late anaphases the centrosome is no longer visible and the spindle fibers are indistinct. There seems to be no resting stage between the first maturation division and the second maturation division.

The chromosomes of the second spermatocyte are ovoid. Metaphase plates show six and seven chromosomes (Figs. 23 and 24). The accessory cannot always be distinguished from the other chromosomes. It is either the second or the third largest. It divides in this division and passes to the poles in advance of the others (Fig. 25). In the late anaphases all the chromosomes have coalesced, although the number may yet be distinguished (Fig. 26). By the time the chromosomes have reached the poles they form a diffuse mass of chromatin at each pole, and the cell has begun to constrict in the middle.

The centrosome which is similar to the centrosome of the primary spermatocyte has disappeared. The spindle fibers have become indistinct. As the constriction of the cell is completed the chromatin has migrated to the center of each daughter cell.

In the changing of the spermatid into the spermatozoon two things are conspicuous from the beginning, the changes in the character of the chromatin and the elongation of the cell body. From the diffuse irregular mass there is formed an ovate body with the chromatin in a coarsely reticular condition largely around the periphery of it. The cell becomes elongate and larger at one end than at the other. The cytoplasm has changed from the tangled network to fibrillar strands of granules extending longitudinally across the cell. The cell wall is quite distinct. This condition is illustrated in Fig. 29. The spermatid continues to elongate. The nucleus becomes spherical and remains at one end of the spermatid. The more granular cytoplasm lies toward the periphery of the tail-like elongation. There is a portion of the cytoplasm extending from the nucleus through the center of the tail which is more finely granular than the remainder and takes the stain less readily. Part of the chromatin has become massed together, forming a sphere situated to the side of the nucleus near the end of the lightly staining area of the tail. The greater part of the remaining chromatin is dis-

tributed around the periphery of the nucleus (Fig. 30). As the tail becomes longer it becomes thinner and a filament extends from the nodule of the head through the entire length of the tail. Very little cytoplasm now surrounds the head (Fig. 31). Finally the head becomes arrow shaped and stains very intensely. The tail is long and filamentous and stains a little less intensely than the head. The head and a portion of the tail are illustrated by Fig. 32. The tail is more than four times as long as is shown in the figure.

McClung ('14) says: "It seems very evident that in the spermatogonia of the Acrididæ we are dealing with a chromosome complex of a very definite and precise organization which, in the great majority, presents itself without essential variation in number, size and form, fiber attachment, arrangement in the metaphase and behavior during division of its elements. *Stenobothrus* and *Pamphagus* seem to be definite exceptions in some of these respects. . . ." And again he says:

"With the exception of the *Stenobothrus*-like species, and *Pamphagus*, the students of the Acrididæ have reported a reduction of the 23 spermatogonial chromosomes to 12."

All of the genera of the family Acrididæ¹ discussed in McClung's paper belong to the three subfamilies, Tryxalinæ, Œdipodinæ, and Acridinæ, and none belong to the subfamily Tettiginæ. It would seem that with the general agreement of the great numbers of genera of this family which he and his students have studied as well as those of other independent workers that he would be justified in making the general statements concerning the family. However, *Paratettix leuconotus-leucothorax* of the subfamily Tettiginæ, show some exceptions. The spermatogonial number of chromosomes are thirteen instead of twenty-three. The number of chromosomes in the primary spermatocyte is seven. This the writer has found to be true also for both the parent forms of the hybrid as well as for others belonging to the genus *Paratettix*.

¹ The writer is aware of the fact that there has been much shifting about of names of the short-horned grasshoppers and that some taxonomists consider the grouse locusts of family value. If this should be the position which McClung takes, then he would not consider *Paratettix* as belonging to the family Acrididæ and it would follow that the observations recorded in this paper would not be exceptions to his statements concerning Acrididæ.

Robertson ('15) says: "In the Tettigidae (Tettiginæ) a subfamily of the short-horned grasshopper family Acrididae, I have found for all the specimens of at least four different genera which I have examined the number of chromosomes to be uniformly 14 in the female and 13 in the male."

From the above data one would scarcely be justified in saying that the characteristic number of spermatogonial chromosomes of the subfamily Tettiginæ is thirteen but the writer feels justified in saying that this is an essential variation in the number of chromosomes given in the above quotation from McClung as the number characteristic for the family Acrididae. The writer has found no indication of multiple chromosomes.

In the prophase tetrad six of the chromosomes are always dumb-bell-shaped and one ovoid. There are none of the irregular shaped chromosomes as described by McClung and no indications of the annular chromosomes which he says "that practically without exception every investigator of recent years who has made a careful study of the maturation stages in the Orthoptera has seen and figured." If the dumb-bell-shaped chromosomes are similar to his I-shaped chromosomes they differ in that they do not have an enlargement in the middle, but rather they have the appearance of a constriction. This constriction is not due to the initiation of the division, for it is present before the chromosomes are arranged on the spindle; in fact, they have their characteristic shape before the spindle is visible.

The presence of a mass of chromatin in the resting stage of the spermatogonial divisions which is of a different form and different staining capacity and also the presence of a similar mass in the growth period, which can be identified as the accessory chromosome of the spermatocyte, gives added evidence for the continuity of chromosomes as definite entities.

The spermatozoön of *Paratettix leuconotus-leucothorax* is very different from the spermatozoön of *Paratettix cuculatus* as described by Hancock. He describes and figures the head of *P. cuculatus* as being small, thin, and acutely pointed. In fact, from his figure one would think that the head is very little thicker than the tail. He says that the middle piece is formed into a

high, rather short, protoplasmic keel. No keel has been observed as forming a part of the middle piece of *P. leuconotus-leucothorax*. The head is many times thicker than the tail and is decidedly arrow shaped. The middle piece seems to continue from the head to the long filamentous tail without a definite dividing line between them.

SUMMARY.

1. *Paratettix leuconotus-leucothorax* has thirteen spermatogonial rod-shaped chromosomes, four larger and nine smaller ones.

2. Neither the larger nor the smaller chromosomes form equal sized pairs.

3. The four larger chromosomes and one of the smaller ones are bent rods, the others are almost straight.

4. Neither spermatogonial chromosome has been surely identified as the accessory chromosome.

5. In the growth period is a mass of chromatin which is more compact and stains more intensely than the remainder of the chromatin. This is the accessory chromosome of the first spermatocyte.

6. The first spermatocyte chromosomes are formed in vesicles.

7. There are six dumb-bell-shaped bivalent chromosomes and one ovoid univalent chromosome in the primary spermatocyte.

8. The accessory is near the periphery of the nucleus and passes to one pole undivided slightly in advance of the other chromosomes in the first spermatocyte division.

9. The bivalent chromosomes divide crosswise.

10. The accessory chromosome divides in the second division.

11. The spermatozoön has an arrow-shaped head and a long filamentous tail.

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EXPLANATION OF PLATES.

All figures were made at table level by means of a Zeiss compensating ocular No. 6 and a 1.5 mm. objective with the aid of a camera lucida. The drawings were enlarged two diameters and then reduced one third.

PLATE I.

FIG. 1. Early prophase of spermatogonial division. A, a mass of chromatin which does not become reticular but remains more or less compact.

FIG. 2. Formation of spermatogonial chromosomes.

FIGS. 3 TO 6. Metaphase plates of spermatogonial chromosomes.

FIG. 7. Metaphase, lateral view, spermatogonial division showing position of the chromosomes on the spindle.

FIG. 8. Anaphase of spermatogonial division.

FIG. 9. Beginning of the growth period. A, a mass of chromatin which does not pass into a reticular condition and forms the accessory chromosome.

FIG. 10. Formation of chromatin thread.

FIG. 11. Synizesis.

FIG. 12. Beginning of the formation of the primary spermatocyte chromosomes.

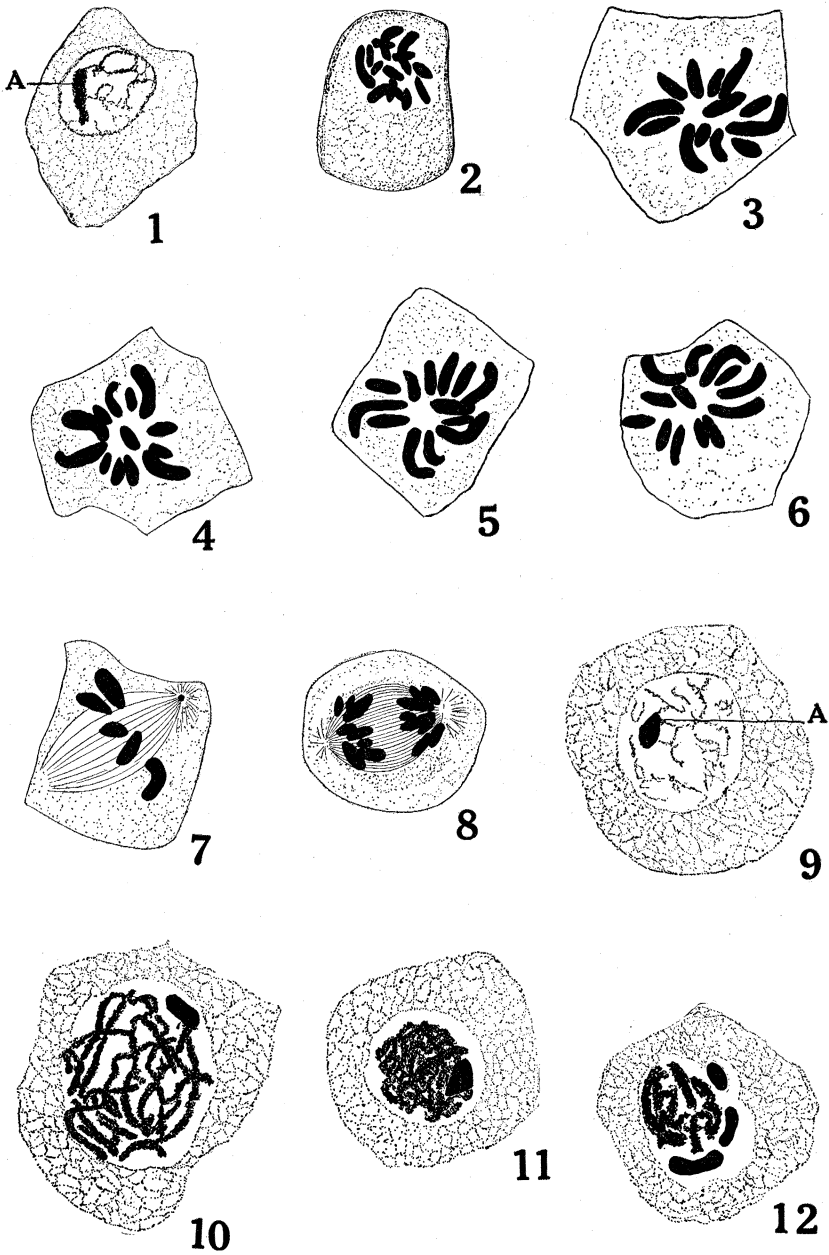


PLATE II.

FIG. 13. Primary spermatocyte chromosomes showing the beginning of the formation of the vesicles.

FIG. 14. Primary spermatocyte chromosomes in vesicles.

FIGS. 15 AND 16. Metaphase, lateral view, of first spermatocyte division. The accessory chromosome is at the periphery of the spindle.

FIGS. 17 AND 19. Metaphase plates of first spermatocyte division showing seven chromosomes.

FIG. 18. Metaphase plate of first spermatocyte division showing six chromosomes. The accessory chromosome is not in the metaphase plate.

FIG. 20. Beginning anaphase of first spermatocyte division.

FIG. 21. Late anaphase of first spermatocyte division showing seven chromosomes.

FIG. 22. Metaphase, lateral view, of second spermatocyte division showing seven chromosomes.

FIG. 23. Metaphase plate of second spermatocyte division showing seven chromosomes.

FIG. 24. Metaphase plate of second spermatocyte division showing six chromosomes.

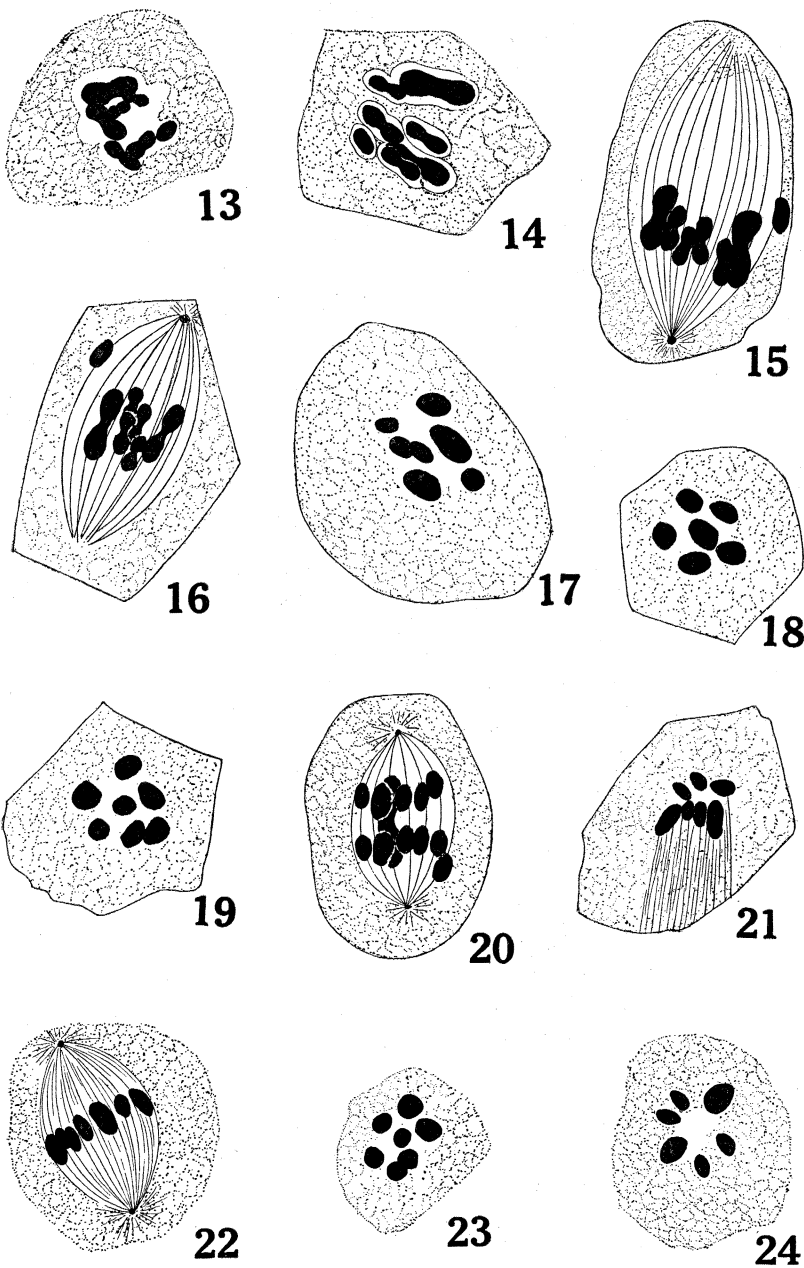


PLATE III.

FIG. 25. Anaphase of second spermatocyte division showing seven chromosomes going to each pole.

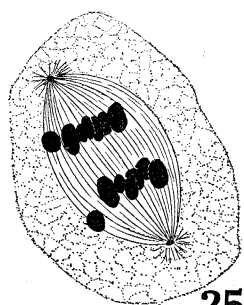
FIG. 26. Late anaphase of second spermatocyte division.

FIG. 27. Telophase of second spermatocyte division.

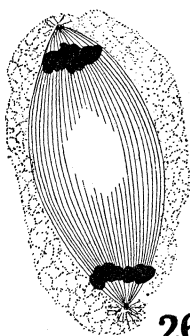
FIG. 28. Spermatids.

FIGS. 29 TO 31. Stages in the development of the spermatozoön.

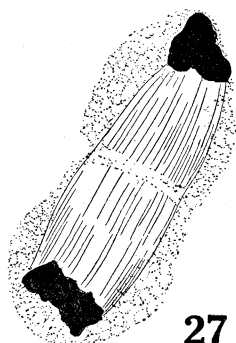
FIG. 32. Head and part of the tail of a spermatozoön.



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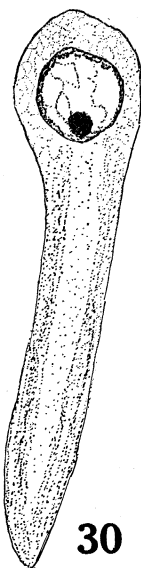
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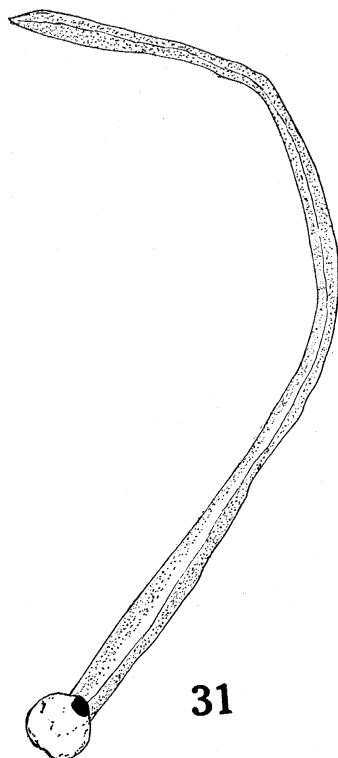
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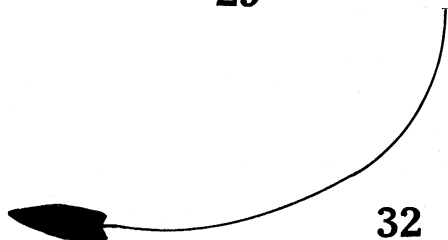
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